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# Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats

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## Abstract

The rapid global spread of artificial light at night is causing unprecedented disruption to ecosystems. In otherwise dark environments, street lights restrict the use of major flight routes by some bats, including the threatened lesser horseshoe bat *Rhinolophus hipposideros*, and may disrupt foraging. Using radio tracking, we examined the response of individual female *R. hipposideros* to experimental street lights placed on hedgerows used as major flight routes. Hedgerows were illuminated on one side over four nights using lights with different emission spectra, while the opposite side of the hedge was not illuminated. Automated bat detectors were used to examine changes in overall bat activity by *R. hipposideros* and other bat species present. *R. hipposideros* activity reduced significantly under all light types, including red light, challenging a previously held assumption that red light is safe for bats. Despite this, *R. hipposideros* rapidly adapted to the presence of lights by switching their flight paths to the dark side of the hedgerow, enabling them to reach foraging sites without restriction. Red light had no effect on the activity of the other species present. Slow-flying *Myotis* spp. avoided orange, white and green light, while more agile *Pipistrellus* spp. were significantly more active at these light types compared to dark controls, most probably in response to accumulations of insect prey. No effect of any light type was found for *Nyctalus* or *Eptesicus* spp. Our findings demonstrate that caution must be used when promoting forms of lighting that are thought to be safe for wildlife before they are tested more widely. We argue that it is essential to preserve dark corridors to mitigate the impacts of artificial light at night on bat activity and movements.

## KEYWORDS

artificial light at night, bats, behaviour, dark corridors, *Rhinolophus hipposideros*, street lights

## 1 | INTRODUCTION

Continued growth in the use of artificial light at night ranks among the most important global threats to biodiversity (Davies & Smyth, 2017;

Gaston, Duffy, Gaston, Bennie, & Davies, 2014; Gaston, Visser, & Hölker, 2015). Nearly one quarter of the world's land surface inhabited by humans now experiences light-polluted nights (Falchi et al., 2016), with artificially lit areas growing on average by two per cent each year,

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both in radiance and extent (Kyba et al., 2017). In Europe, as much as 88% of the land surface is affected by light pollution (Falchi et al., 2016). Negative impacts of lighting have been demonstrated for a wide variety of organisms, with effects observed at all levels of biological complexity from gene expression to ecosystem functioning (Bennie, Davies, Cruse, & Gaston, 2016; Bennie, Duffy, Davies, Correa-Cano, & Gaston, 2015; Davies, Bennie, & Gaston, 2012; Fonken & Nelson, 2014; Gaston, Bennie, Davies, & Hopkins, 2013; Honnen, Johnston, & Monaghan, 2016; Lewanzik & Voigt, 2014). Strictly nocturnal animals such as bats are considered most at risk and have been a focus of research in recent years (e.g., Rydell, 1992; Gutierrez, Pessoa, Aguiar, & Pessoa, 2014; Lacoëuilhe, Machon, Julien, Le Bocq, & Kerbiriou, 2014; Lewanzik & Voigt, 2017; Rowse, Harris, & Jones, 2016; Rydell, Eklöf, & Sánchez-Navarro, 2017; Spoelstra et al., 2017; Stone, Jones, & Harris, 2009, 2012).

Street lights are a primary source of light pollution in semi-natural ecosystems. The effects of street lights on bats are varied, and behavioural responses appear to be species-specific. Some fast-flying bats may benefit by exploiting accumulations of positively phototactic insect prey that aggregate at lights and so are considered to be light-opportunistic. The predictability and increase in density of insect prey at street lights combined with the impairment of prey defence mechanisms (Acharya & Fenton, 1999; Minnaar, Boyles, Minnaar, Sole, & McKechnie, 2014; Svensson & Rydell, 1998; Wakefield, Stone, Jones, & Harris, 2015) may improve foraging efficiency for light-opportunistic bats, and the activity of bats recorded regularly at street lights, such as *Pipistrellus* spp., is generally highest at lights that emit short wavelengths, that is those most attractive to insects (Blake, Hutson, Racey, Rydell, & Speakman, 1994; Rydell, 1992; Spoelstra et al., 2017; Stone, Wakefield, Harris, & Jones, 2015), supporting the hypothesis that bats are drawn to street lights primarily for foraging.

In contrast, slower-flying bats, which are thought to be more vulnerable to predation by aerial-hawking birds that hunt by vision, are typically light-averse (Spoelstra et al., 2017; Stone, Jones, & Harris, 2009, 2012). The deterrence effect of artificial light on light-averse bats has been demonstrated at roosts (Boldogh, Dobrosi, & Samu, 2007; Rydell et al., 2017; Zeale et al., 2016) and at habitats used for commuting and foraging (Azam et al., 2018; Spoelstra et al., 2017; Stone, Jones, & Harris, 2009, 2012), and this effect is consistent across a range of lighting technologies (Spoelstra et al., 2017; Stone, Jones, & Harris, 2009, 2012). Previous experiments found that both high-pressure sodium (HPS) (Stone, Jones, & Harris, 2009) and white light-emitting diode (LED) lights (Stone, Jones, & Harris, 2012) restricted the use of major flight routes by threatened lesser horseshoe bats *Rhinolophus hipposideros*, raising concern about their ability to reach preferred foraging sites and feed during hours of peak insect activity. In the absence of data on the wider movements of individual bats, however, it was not possible to establish the impact on factors that may affect fitness, such as ranging behaviour and habitat selection. This is an important knowledge gap that must be addressed if we are to understand the conservation implications of light pollution on bats.

As evidence for the detrimental impacts of artificial light at night continues to grow, attention is now turning towards how best to mitigate its ecological effects. New lighting technologies allow for greater flexibility in the control of light emissions from individual street lights, and so options such as dimming, part-night lighting and altering the spectrum of lights are being explored (Azam et al., 2015; Day, Baker, Schofield, Matthews, & Gaston, 2015; Gaston, Davies, Bennie, & Hopkins, 2012; Rowse, Harris, & Jones, 2018; Spoelstra et al., 2017). While dimming and part-night lighting are useful in reducing light pollution overall, the opportunity to deliver benefits for bats may be limited. Significant reductions in activity by *Myotis* and *Rhinolophus* spp. occur under broad-spectrum LEDs even when light levels are considerably lower than those typically used for public street lighting (Stone et al., 2012). In addition, as street lights typically remain switched on during the hours around dusk and dawn when bat activity is highest, the majority of current part-night lighting schemes are unlikely to deliver significant benefits for bats (Azam et al., 2015; Day et al., 2015; Gaston et al., 2012).

Studies examining the response of bats to different light spectra are limited, but there are spectrum-dependent effects among both light-opportunistic and light-averse bats (Spoelstra et al., 2017). Spoelstra et al. (2017) found *Pipistrellus* spp. were significantly more active around white and green light compared to dark controls, but equally active in red light and darkness. In contrast, *Myotis* and *Plecotus* spp. avoided white and green light but were also equally active in red light and darkness, raising the possibility that red light may be used to mitigate the impact of light pollution on bats (Spoelstra et al., 2017). However, it is unclear whether these results are applicable to other species of bat.

In this study, we examine the response of the light-averse bat *R. hipposideros* to street lights with different emission spectra, including red light. In addition to acoustic monitoring of bat activity, we use radio tracking to examine the impact of lights on individual *R. hipposideros*. Ranging behaviour and habitat use can be quantified using radio tracking and are likely to affect fitness and so provide better measures of the impact of lighting than bat activity recorded on detectors. We illuminated one side of the hedgerow while keeping the other side in darkness to investigate the extent to which the preservation of dark corridors can mitigate the impacts of lighting. This is the first study that we are aware of to examine the response of individual bats to street lighting, providing new insight into the ability of bats to adapt to novel sources of light pollution in their environment.

## 2 | MATERIALS AND METHODS

### 2.1 | Light types

We examined the response of bats to four types of street light: high-pressure sodium (HPS) (DW Windsor Ltd, Hertfordshire, England), neutral white light-emitting diode (LED) (CU Phosco, Hertfordshire, England), and two induction lamps that emit narrowband wavelengths predominantly in the green and red part of the visible

spectrum (QL Company, Vessel, Netherlands), hereafter referred to as orange, white, green and red light, respectively. Images of each light type in situ during experiments and their respective emission spectra are provided in Supporting Information Figure S1. We used HPS lights as these were among the most widely used light types in Europe prior to the widespread installation of neutral white LEDs.

Irradiance measurements for each light type were recorded in a dark room at the University of Bristol using a cosine corrector attached to a 400 µm diameter UV-visible fibre-optic cable. The cable was connected to a spectrometer (USB2000, Ocean Optics, FL, USA) controlled by a PC running SpectraSuite (v. 6, Ocean Optics). A Gershun tube was used to reduce the acceptance angle, that is the amount of light that falls on the sensor, to ensure that irradiance measurements were only recorded for photons emitted directly from the lights.

## 2.2 | Lighting experiments

Experiments were undertaken on hedgerows used as major commuting routes by *R. hipposideros* at eight maternity roosts in south-west England and Wales between July and September 2014. We selected sites located within dark agricultural landscapes comprising predominantly pasture, semi-natural woodland and low- to medium-density housing. Each experiment lasted for five nights: A single dark control night with street lights in situ but switched off was followed by four consecutive nights illuminated using the four light types. The order of light types was randomized across sites to control for order effects of light treatments.

Prior to installing street lights, acoustic monitoring surveys were undertaken on all hedgerows around maternity roosts to determine relative levels of bat activity. Two portable street light columns were installed the following day on the hedgerow with the highest recorded *R. hipposideros* activity, hereafter referred to as the experimental hedge. The columns were positioned 30 m apart, mimicking the spacing commonly used for public street lights in the UK (Stone et al., 2009), and at each site, the lights were located between 100 and 300 m from the *R. hipposideros* roost (mean  $168.1 \pm 67.0$  m). Lights were powered by a Honda EU26i portable silenced generator (Honda UK, Slough, UK) located at least 50 m from the experimental hedge. On each treatment night, the lights were switched on 30 min before sunset and switched off 30 min after sunrise. Previous experiments using a similar experimental set-up showed that the generator had an audible noise output of 49 dB at 7 m and did not affect bat activity when positioned 50 m from the experimental hedge (Stone, Jones, & Harris, 2009, 2012).

Hedges were illuminated on one side to a mean light level of  $55.01 \pm 3.90$  lx. This is within the range used during previous experiments using orange HPS (Stone et al., 2009) and white LED (Stone et al., 2012) light and is equivalent to that emitted by public street lights in the UK (Stone et al., 2009). Hedges were sufficiently high (mean height  $6.7 \pm 4.1$  m) and densely vegetated to control light spill, such that the opposite side of the hedge remained comparatively dark ( $0.74 \pm 0.73$  lx). Illuminance (in lux) was measured using a

T-10 illuminance meter (Konica Minolta Sensing Inc., Osaka, Japan) held 1.75 m above ground level at the hedge below the lights and at the same position on the opposite side of the hedge. The illuminance meter was held horizontally, such that the sensor was pointed directly upwards towards the light source. A weather station (Tycon Systems Inc., Bluffdale, USA) was positioned in open ground within 50 metres of the experimental hedge to record total nightly rainfall, mean nightly temperature and mean nightly wind speed.

## 2.3 | Acoustic monitoring of bat activity

We used Song Meter SM2BAT+ Bat Recorders (Wildlife Acoustics Inc., MA, USA) to monitor bat activity on each side of the experimental hedge from 30 min before sunset to 30 min after sunrise. Bat echolocation calls were recorded in full spectrum using the following detector settings: sample rate 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 s; and trigger level 18 dB. Calls were analysed in BatSound v.4 (Pettersson Elektronik, Uppsala, Sweden) and identified manually to species using call parameters described in Russ (2012) or to a species group when calls lacked diagnostic features. Calls were grouped into four species/species groups: *R. hipposideros*, *Myotis* spp., *Pipistrellus* spp. and a group including *Nyctalus* and *Eptesicus* spp. Other rarely recorded species, including *Barbastella barbastellus*, *Plecotus* spp. and *Rhinolophus ferrumequinum* (total 100 passes; 0.2% of overall bat activity), were removed from the dataset.

We identified a bat pass as a call sequence containing three or more pulses and when the time between calls exceeded four times the inter-pulse interval (Parsons & Jones, 2000). Feeding activity by *Pipistrellus* spp. under control and light treatments was examined by identifying diagnostic terminal feeding buzzes within recordings. These highly frequency-modulated calls are emitted at high repetition rates by bats when attempting to capture prey (Kalko, 1995). Relative feeding activity was measured using a “buzz ratio,” calculated as the proportion of feeding buzzes to bat passes recorded each night.

## 2.4 | Radio tracking and analysis of spatial data

We used radio tracking to determine the home range areas and habitat preferences of adult female *R. hipposideros* during each night of the experiment. At least two nights prior to beginning the experiments, bats were caught using handheld nets as they emerged from the roost at dusk and their reproductive state determined to ensure that neither heavily pregnant nor lactating females with dependent young were tagged (Mitchell-Jones & McLeish, 2004). Radio tags (PicoPip Ag337, 0.31 g; Biotrack Ltd, Wareham, UK) weighing <6.5% of body weight were fitted between the scapulae of 12 adult female bats at each site using an ostomy adhesive solution (Salts Healthcare, Birmingham, UK). Bats were followed each night using a R1000 receiver (Communications Specialists Inc., Orange, CA, USA) and a 3-element Yagi antenna, and locational fixes recorded every 5–10 min between dusk and dawn using the “homing-in” method (Davidson-Watts, Walls, & Jones, 2006; Jones & Morton, 1992; White &

Garrott, 1990; Zeale, Davidson-Watts, & Jones, 2012) to examine foraging behaviour. Any night with less than 90% contact time with a bat was excluded as we could not identify the complete pattern of movements throughout the night. Experiments were performed under licence from Natural England (licence number 20,120,837), and the study was approved by the University of Bristol's Home Office Liaison Team and Ethical Review Group.

Home range areas were calculated after plotting radio fixes in ArcGIS 10 (Esri Inc., Redland, CA, USA). Fix data were imported into Ranges 7 (Anatrack Ltd, Wareham, Dorset, UK) and used to calculate individual home range areas (100% minimum convex polygons; MCPs) and core foraging areas (cluster cores) (Davidson-Watts et al., 2006; Zeale et al., 2012). Analysis of utilization distribution discontinuities (Kenward, 2001) showed that up to 15% of fix locations increased the size of foraging areas disproportionately, and, since examination of these fixes revealed that they were primarily recorded as bats commuted between roosts and foraging areas, 85% cluster cores were used to define core foraging areas.

Habitat preferences were examined by comparing the habitat composition of core foraging areas (85% cluster cores) to that available (100% MCPs) (Davidson-Watts & Jones, 2006; Davidson-Watts et al., 2006; Zeale et al., 2012). Compositional analysis (Compositional Analysis Plus Microsoft Excel tool 6.2, Smith Ecology Ltd, Abergavenny, Gwent, UK) was used to determine whether habitats were used in proportion to their availability or whether selection was occurring and to rank habitat types (Aebischer, Robertson, & Kenward, 1993). Habitat data were extracted from digital maps developed in-house using ArcGIS 10 and the five broad habitat categories described in Supporting Information Table S1.

## 2.5 | Statistical analysis

Analyses were performed in R v.3.4.2 (R Core & Team, 2016) using the significance level  $p < 0.05$ . We found no difference in mean nightly temperature ( $F_{4,35} = 0.26$ ,  $n = 8$  sites,  $p = 0.90$ ), total nightly rainfall ( $F_{4,35} = 1.01$ ,  $n = 8$  sites,  $p = 0.41$ ) or mean nightly wind speed ( $F_{4,35} = 0.53$ ,  $n = 8$  sites,  $p = 0.71$ ) among treatment nights, and so these variables were excluded from further analyses to achieve model simplification. To examine the effect of light type on bat activity, we fitted repeated measures generalized linear mixed effects models with a negative binomial distribution to counts of bat passes for each species group on each side of the experimental hedge using the glmer.nb routine in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Treatment type was included as a fixed effect while site was included as a random effect to control for variation between sites. We fitted the same model to counts of feeding buzzes to examine the effect of light type on feeding activity by *Pipistrellus* spp. and fitted a logistic regression model with a binomial distribution to buzz ratio (proportion) data using the glmer routine in lme4. Full and reduced models with and without light treatment were compared using the lrttest routine in the lmerTest package (Zeileis & Hothorn, 2002). Post hoc pairwise comparisons of treatment types were made using the lsmeans package (Lenth, 2016) with Bonferroni-corrected probabilities.

To determine whether the presence of lights on commuting routes affected the ranging behaviour of *R. hipposideros*, we used the lmer routine in lme4 to fit linear mixed effects models with a Gaussian distribution to three response variables derived from radio tracking data: home range area (100% MCP), core foraging area (85% cluster core) and maximum range span (distance from roost to furthest edge of core foraging area). Site and bat were included as random factors, with bat nested within site to control for variation among sites and bats. Finally, to examine whether the location of core foraging areas differed under each light treatment, we calculated the per cent overlap of core foraging areas for control–light treatment pairs for each bat under each light type using

$$\frac{(\frac{O}{C}) + (\frac{O}{L})}{2}$$

where a dark control core foraging area C and a light treatment core foraging area L overlap each other by area O and fitted the same linear mixed effects model to these data. Where necessary, response variables from radio-tracked bats were transformed to meet the assumptions of homoscedasticity and normality (Altman, 1991). Underlying data are available at the University of Bristol data repository, data.bris, at <https://doi.org/10.5523/bris.31dvq1elivhby2dap2tm0zg94>.

## 3 | RESULTS

### 3.1 | Bat activity at experimental hedges

We recorded a total of 57,558 bat passes on experimental hedges during the 40 nights of monitoring. Most records were of *Pipistrellus* spp. (49,465 passes; 85.9%), followed by *R. hipposideros* (5,085; 8.8%), *Nyctalus* and *Eptesicus* spp. (2,133; 3.7%) and *Myotis* spp. (875; 1.5%). We found significant effects of street lights on bat activity for all species groups except *Nyctalus* and *Eptesicus* spp., which showed similar activity levels across treatment types (Table 1). *Rhinolophus hipposideros* activity declined significantly on the lit side of the experimental hedge under all light types compared to the dark control night, with white light having the strongest, and red light the weakest, effect (Figure 1). The reduction in passes on the lit side of the hedge was mirrored by a corresponding significant increase in passes on the opposite dark side of the hedge for all light types (Figure 1).

*Myotis* spp. activity declined significantly on the lit side of the experimental hedge under orange, white and green light compared with the dark control night (Figure 2). Their activity also declined under red light, but the effect was not significant (Figure 2). We found no significant effect of any light type on the activity of *Myotis* spp. on the dark side of the hedge (Table 1; Supporting Information Table S2). Activity by *Pipistrellus* spp. increased significantly on the lit side of the hedge under orange, white and green light, with the greatest activity recorded under green light (Figure 2). A comparatively small increase in activity under red light was not significant (Figure 2). The same response for *Pipistrellus* spp. was observed on the dark side of the hedge (Table 1; Supporting Information Table S2). The number of feeding buzzes emitted by *Pipistrellus* spp. increased significantly under



**TABLE 1** Results from negative binomial generalized linear mixed effects model comparisons with and without light treatment for bat activity (passes) and *Pipistrellus* spp. feeding activity (buzzes), and logistic regression models with binomial distribution for *Pipistrellus* spp. buzz ratio data (number of feeding buzzes divided by the number of passes). In each model, light treatment (treatment) was included as a fixed effect while site (site) was included as a random factor

	df	AIC	loglik	df	$\chi^2$	p
Bat activity (passes)						
<i>Rhinolophus hipposideros</i> (lit side)						
Site	3	403.04	−198.52			
Treatment + Site	7	385.99	−186.00	4	25.05	<0.0001
<i>R. hipposideros</i> (unlit side)						
Site	3	400.86	−197.43			
Treatment + Site	7	389.55	−187.78	4	19.31	<0.001
<i>Myotis</i> spp. (lit side)						
Site	3	268.12	−131.06			
Treatment + Site	7	255.97	−120.99	4	20.15	<0.001
<i>Myotis</i> spp. (unlit side)						
Site	3	266.65	−130.33			
Treatment + Site	7	267.89	−126.95	4	6.76	0.15
<i>Pipistrellus</i> spp. (lit side)						
Site	3	606.50	−300.25			
Treatment + Site	7	576.53	−281.26	4	37.97	<0.0001
<i>Pipistrellus</i> spp. (unlit side)						
Site	3	569.85	−281.93			
Treatment + Site	7	551.26	−268.63	4	26.59	<0.0001
<i>Nyctalus and Eptesicus</i> spp. (lit side)						
Site	3	278.71	−136.36			
Treatment + Site	7	284.46	−135.23	4	2.26	0.69
<i>Nyctalus and Eptesicus</i> spp. (unlit side)						
Site	3	273.69	−133.85			
Treatment + Site	7	278.17	−132.09	4	3.52	0.47
<i>Pipistrellus</i> spp. feeding activity						
Number of buzzes (lit side)						
Site	3	417.82	−205.91			
Treatment + Site	7	394.01	−190.01	4	31.81	<0.0001
Buzz ratio (lit side)						
Site	2	433.12	−214.56			
Treatment + Site	6	436.71	−212.35	4	4.41	0.35

all light types compared to dark control nights, except under red light where the increase was not significant (Table 1; Supporting Information Table S2). We found no difference in buzz ratio among treatment types, demonstrating that feeding activity increased in proportion with overall activity under each light type.

### 3.2 | Response of radio-tagged bats

We tagged a total of 96 *R. hipposideros* across the eight study sites. We obtained radio tracking data for the dark control night and each

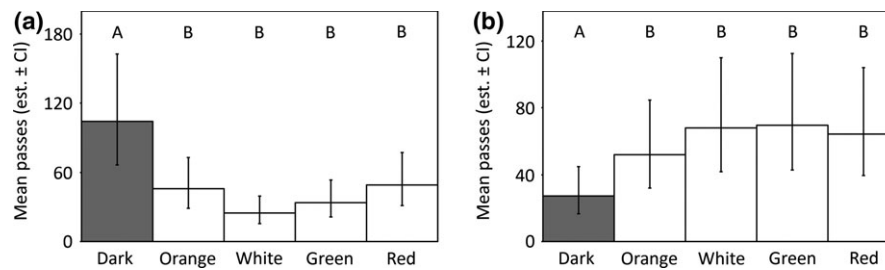
of the four light treatments from at least eight bats at each site. Incomplete data sets for individual bats were due to loss of radio contact or tag failure and were excluded from the analyses. On average, we obtained  $54.0 \pm 11.2$  fixes from each bat on each night of our experiments. Range data for dark control nights (Table 2) show that, on average, bats foraged at a distance of  $2.0 \pm 0.9$  km from the maternity roost and used only  $14.3\% \pm 7.6\%$  of their individual 100% MCP for foraging. Bats foraged in similar-sized (mean  $17.6 \pm 5.4$  ha) core foraging areas that were largely spatially separated. An example of the type of spatial organization exhibited by radio-tracked bats is provided in Figure 3.

When we fitted linear mixed models to the spatial data (Table 3), we found no effect of treatment type on any of the variables tested, that is bats foraged in similar-sized core foraging areas that were located in the same place and travelled similar distances to reach their core foraging areas during dark control and light treatment nights. Compositional analysis to determine habitat preferences revealed that bats consistently preferred to forage in woodland above all other habitat types (Table 4). Grassland and riparian habitats were the next most preferred habitats. Arable and built-up areas consisting mainly of medium-density residential housing were least preferred. We observed no difference in habitat preferences between treatment types (Table 4).

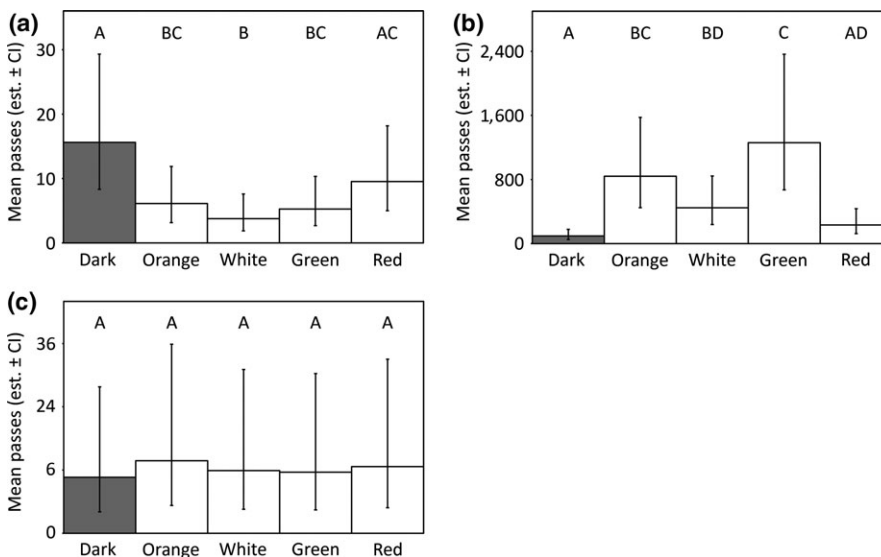
## 4 | DISCUSSION

Vegetation corridors such as hedgerows provide important movement and dispersal pathways for wildlife and the loss of these pathways, either through direct removal or disturbance, for example from artificial lighting, poses a significant threat to bats (Lacoeuilhe, Machon, Julien, & Kerbiriou, 2016). Here, we show that *R. hipposideros* is significantly deterred from using hedgerow commuting routes when street lights are introduced. The effect is consistent across a range of light types, including red light, demonstrating that red light may be safe for bats only in specific circumstances. (Spoelstra et al., 2017; Spoelstra, Ramakers, van Dis, & Visser, 2018). Despite being deterred, *R. hipposideros* adapted quickly by switching flight paths and exploiting dark corridors on the opposite side of experimental hedges. As a result, we observed no effect of our street light set-up on the ranging and foraging behaviour of radio-tracked *R. hipposideros*. The home range sizes of bats in this study and the preference for foraging in woodland are consistent with previous studies (Bontadina, Schofield, & Naef-Daenzer, 2002; Downs et al., 2016; Knight, 2006; Zahn, Holzhaider, Kriner, Maier, & Kayikcioglu, 2008).

Our findings suggest that hedgerow commuting routes will become unsuitable for *R. hipposideros* if illuminated on both sides. Stone et al. (2012) demonstrated that *R. hipposideros* is deterred by white LED street lights at illuminances of 3.6 lx. Other species, such as *Myotis* spp., are deterred below 1 lx (Azam et al., 2018), and so even low levels of light can significantly disrupt the behaviour of light-averse bats. To minimize impacts on *R. hipposideros*, we recommend that light trespass on hedgerow commuting routes should not



**FIGURE 1** Mean number of passes made by *Rhinolophus hipposideros* on (a) the lit side and (b) the unlit side of experimental hedges ( $n = 8$  sites) during dark control and four light treatment nights using orange, white, green and red light. Data are back-transformed treatment estimates from negative binomial generalized linear mixed effects models with treatment as a fixed effect and site as a random effect. Letters above bars identify treatments that differ significantly from each other in post hoc tests (Supporting Information Table S2)



**FIGURE 2** Mean number of passes made by (a) *Myotis* spp., (b) *Pipistrellus* spp. and (c) *Nyctalus* and *Eptesicus* spp. on the lit side of experimental hedges ( $n = 8$  sites) during dark control and four light treatment nights using orange, white, green and red light. Data are back-transformed treatment estimates from negative binomial generalized linear mixed effects models with treatment as a fixed effect and site as a random effect. Letters above bars identify treatments that differ significantly from each other in post hoc tests (Supporting Information Table S2)

**TABLE 2** Mean home range areas (100% MCPs), core foraging areas (85% cluster cores) and range spans (mean maximum nightly distance from roost to furthest edge of 85% cluster core) for 64 adult female *Rhinolophus hipposideros* from eight maternity roosts ( $n = 8$  bats per site) radio-tracked before (dark) and during four light treatments

Night	Home range area (ha) <sup>a</sup>	Foraging area (ha) <sup>a</sup>	Range span (km) <sup>a</sup>
Dark	157.8 ± 98.9	17.6 ± 5.4	2.0 ± 0.9
Orange	158.5 ± 104.9	18.0 ± 5.4	2.1 ± 0.9
White	153.1 ± 98.4	18.1 ± 5.4	2.1 ± 0.8
Green	154.2 ± 109.1	17.7 ± 5.9	2.0 ± 0.8
Red	156.4 ± 92.4	17.2 ± 5.4	2.1 ± 0.8

<sup>a</sup>Mean ± standard deviation.

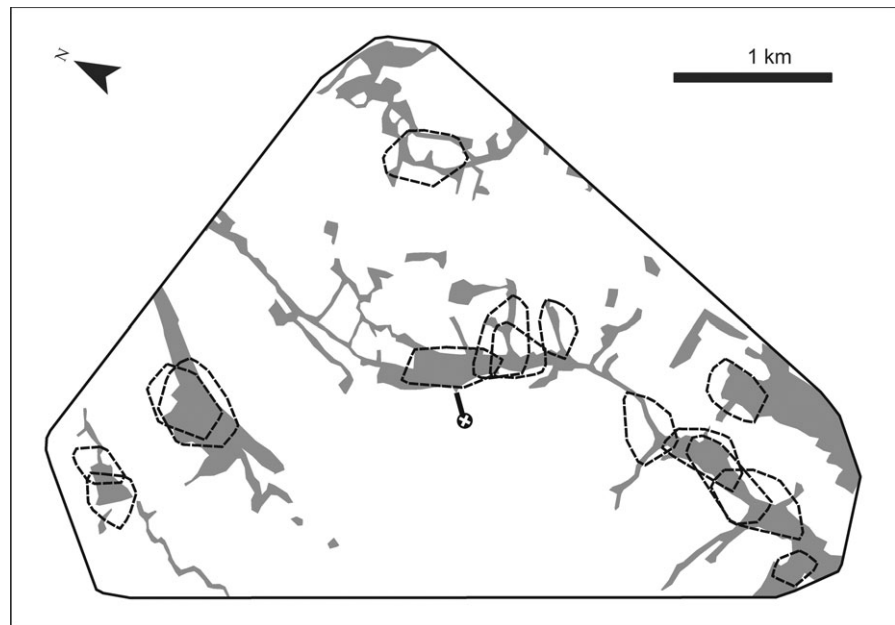
exceed that recorded on the dark side of our experimental hedges (0.74 lx). If *R. hipposideros* is forced to use alternative flight routes, this may have fitness consequences, particularly if alternative routes limit access to foraging sites or provide poorer cover from predatory birds (Boughey, Lake, Haysom, & Dolman, 2011; Hein, Castleberry, & Miller, 2009; Lacoëuilhe et al., 2016; Verboom & Huitema, 1997). In this study, hedgerows with the highest *R. hipposideros* activity

were most often those that provided the shortest and most direct route from roosts to the nearest available woodland (e.g., Figure 3), and so it is important that these flight lines in particular are protected from light pollution and managed to provide vegetation cover that maximizes benefits for bats (Boughey et al., 2011).

Among the other bat species recorded at experimental hedges, *Myotis* spp. were deterred by orange, white and green lights, but not by red light. Similarly, Spoelstra et al. (2017) found *Myotis* and *Plecotus* spp. to be deterred by white and green, but not red, light. Aversion to light appears to be common among slow-flying *Myotis* spp., and, in extreme cases, artificial lighting has entombed bats within roosts (Zeale et al., 2016). While bats appear to be sensitive to wavelengths throughout the visible spectrum (Wang et al., 2004; Zhao et al., 2009), they may be relatively more sensitive to shorter wavelengths, and this could explain the greater tolerance of longer-wavelength red light by some light-averse species (Müller et al., 2009; Spoelstra et al., 2017).

Unlike *R. hipposideros*, we did not find a corresponding increase in activity by *Myotis* spp. on the dark side of experimental hedges when they were deterred by lights on the lit side, that is *Myotis* spp. appeared to move away from the site when deterred, probably because *Myotis* spp. were recorded sporadically during the night

**FIGURE 3** Example of the spatial organization of core foraging areas (dashed line polygons) used by *Rhinolophus hipposideros* ( $n = 8$  bats) in relation to the roost (white cross) and experimental hedge (black line from roost). Some bats had multiple core foraging areas. Woodland is shown as grey shaded areas, encompassed by the colony home range area (solid line polygon) that delimits all radio tracking fixes recorded for all bats. Data presented are for the dark control night prior to illuminating the experimental hedge with street lights



**TABLE 3** Results from linear mixed effects model comparisons with and without light treatment for four measures of *Rhinolophus hipposideros* ranging and foraging behaviour derived from radio tracking data: (a) size of 100% MCP home range area, (b) size of 85% cluster core foraging area, (c) maximum range span (distance from roost to furthest edge of core foraging area) and (d) per cent overlap of core foraging areas for control–light treatment pairs. In each model, light treatment (treatment) was included as a fixed effect while site and bat were included as random factors, with bat nested within site (site/bat)

Spatial data	df	AIC	loglik	df	$\chi^2$	p
log Home range area						
Site/Bat	4	−12.99	10.47			
Treatment + Site/Bat	8	−8.33	12.17	4	3.39	0.50
sqrt Core foraging area						
Site/Bat	4	368.87	−180.43			
Treatment + Site/Bat	8	372.90	−178.45	4	3.97	0.41
log Maximum range span						
Site/Bat	4	−779.02	393.51			
Treatment + Site/Bat	8	−774.02	395.01	4	3.01	0.56
Core foraging area overlap						
Site/Bat	4	4487.70	−2239.90			
Treatment + Site/Bat	7	4493.30	−2239.70	3	0.41	0.94

suggesting low-level use of sites for foraging. In contrast, *R. hipposideros* activity remained largely stable at experimental hedges across treatment nights, even when bats were deterred from the lit side, probably due to the higher dependency of *R. hipposideros* on these sites as important commuting routes linking roosts to foraging areas. Even so, *Myotis* spp. activity on the dark side of the hedgerow remained stable during lit treatments, indicating that good management of light spill, can mitigate disturbance to both *R. hipposideros* and *Myotis* spp.

We found *Pipistrellus* spp. to be significantly more active around orange, white and green light compared to dark controls, but equally active in red light and darkness, as reported by Spoelstra et al. (2017). We observed the same response by *Pipistrellus* spp. on both the lit and dark side of experimental hedges, probably because (a) the flight paths of *Pipistrellus* spp. foraging in and around the light cones of streetlights intersected hedges, and (b) the echolocation calls of *Pipistrellus* spp. are sufficiently intense to be detected on both sides of the hedge simultaneously. Similarly, we recorded the same response on both sides of experimental hedges for *Nyctalus/Eptesicus* spp., which also fly above the height of hedges and emit high-intensity calls. In contrast, *R. hipposideros* flies close to vegetation along the sides of hedges and emits high-frequency calls that attenuate rapidly, and so individual *R. hipposideros* are unlikely to be detected simultaneously on both sides of hedgerow commuting routes.

Foraging activity by *Pipistrellus* spp. also increased under orange, white and green light, indicating that these light types provided greater foraging opportunities compared to dark controls. Feeding buzzes increased only in proportion with overall activity, however, indicating that the rate at which *Pipistrellus* spp. attempted to catch insect prey at lights was no higher than in darkness. However, even if foraging efficiency is not significantly improved, the increased predictability of prey resources at street lights is likely to be of benefit.

While Spoelstra et al. (2017) found *Pipistrellus* spp. to be most active in white light, we found activity to be significantly higher in green light. Although we cannot rule out the possibility that bats were attracted to green light by positive phototaxis (Voigt, Roeleke, Marggraf, Pētersons, & Voigt-Heucke, 2017), the green lights used in this study emitted additional short wavelengths that were not emitted by the lights used by Spoelstra et al. (2017) and so may have been more attractive to insects (Barghini & de Medeiros, 2012; Somers-Yeates, Hodgson, McGregor, Spalding, & French-Constant, R. H.,



**TABLE 4** Foraging habitat preferences in 85% cluster cores for 64 adult female *Rhinolophus hipposideros* radio-tracked at eight maternity roosts ( $n = 8$  bats per site) under dark control and orange, white, green and red light treatments. Habitat categories to the left of > are used in higher proportion to those to the right, with >>> showing a significant difference between adjacent habitat types

Treatment	Ranked habitat types								p*	
Dark	Woodland	>	Grassland	»»	Riparian	>	Arable	»»	Urban	<0.001
Orange	Woodland	>	Grassland	»»	Riparian	>	Arable	»»	Urban	<0.001
White	Woodland	>	Grassland	»»	Riparian	>	Arable	»»	Urban	<0.001
Green	Woodland	>	Grassland	»»	Riparian	>	Arable	»»	Urban	<0.001
Red	Woodland	>	Grassland	»»	Riparian	>	Arable	»»	Urban	<0.001

\* $p$ -value < 0.05 shows habitat use is non-random, that is selection of habitats has occurred.

2013; van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011), and therefore also *Pipistrellus* spp.

Other context-dependent factors are also likely to influence foraging behaviour at lights and make direct comparisons between studies difficult. Sonar jamming, for example, is used by some bats when competing with conspecifics for food (Corcoran & Conner, 2014), and some *Pipistrellus* spp. increase their flight speed and fly at lower altitudes when foraging at lights, presumably to mitigate the increased risk of predation at lights (Polak, Korine, Yair, & Holderied, 2011). Further research is needed to better understand how artificial lighting influences interactions between bats and to what extent different species are advantaged or disadvantaged. Where *Pipistrellus* spp. are advantaged, competition for food might contribute to the decline of light-averse species with similar diets, such as *R. hipposideros* (Arlettaz, Godat, & Meyer, 2000). Moreover, light-averse species are typically rarer and of greater conservation concern than their light-opportunistic counterparts (Lacoeuilhe et al., 2014).

We found no effect of lights on the activity of *Nyctalus* and *Eptesicus* spp. and did not observe them foraging at our lights, even though they forage above street lights (Catto, Hutson, Racey, & Stephenson, 1996; Kronwitter, 1988; Rydell, 1992). *Nyctalus* and *Eptesicus* spp. are "open space foragers" (Denzinger & Schnitzler, 2013) and emit low-frequency, high-intensity echolocation calls that can be detected at distances up to 100 metres, so many of our recordings may have been from bats that were not interacting with our experimental set-up. As a result, we urge caution when interpreting our findings for *Nyctalus* and *Eptesicus* spp.

While the use of red light may help to mitigate the impact of artificial light for some species, our findings demonstrate that it is not universally safe for bats and should not always be considered a suitable alternative to preserving dark corridors. Our findings demonstrate that caution must be used when promoting forms of lighting that are thought to be safe for wildlife before they are tested more widely. Preserving dark corridors requires a landscape-scale approach to managing light pollution to ensure that links between important habitats are maintained throughout bat core sustenance zones, that is the area surrounding a communal roost within which habitat availability and quality will have a significant influence on the resilience and conservation status of the bat colony (Bat Conservation Trust, 2016). We argue that a coherent and resilient "nocturnal network," that is a network of areas or habitats without artificial lighting

(Lacoeuilhe et al., 2014), will be necessary to protect bats and other nocturnal animals against the growing impacts of light pollution.

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## CONFLICT OF INTEREST

We declare we have no competing interest.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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